Science of the Total Environment 476–477 (2014) 591–600

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The history of widespread decrease in oak dominance exemplified in a grassland–forest landscape

Brice B. Hanberry [a,*], Daniel C. Dey [b], Hong S. He [a,1]

[a] University of Missouri, 203 Natural Resources Building, Columbia, MO 65211, USA
[b] USDA Forest Service, Northern Research Station, University of Missouri, 202 Natural Resources Building, Columbia, MO 65211, USA

HIGHLIGHTS

- Oak establishment is decreasing and open oak ecosystems are remnants.
- We demonstrate loss of open oak ecosystems across a grassland–forest landscape.
- Oaks decreased from 62% of historical composition to 30% of current composition.
- Current forest densities were two times greater than historical densities.
- Prescribed fire with silvicultural methods may help establish oak.

ARTICLE INFO

Article history:
Received 29 October 2013
Received in revised form 14 January 2014
Accepted 15 January 2014
Available online 1 February 2014

Keywords:
Fire suppression
Historical forest
Land use
Oak restoration
Savanna
Woodland

ABSTRACT

Regionally-distinctive open oak forest ecosystems have been replaced either by intensive agriculture and grazing fields or by denser forests throughout eastern North America and Europe. To quantify changes in tree communities and density in the Missouri Plains, a grassland–forest landscape, we used historical surveys from 1815 to 1864 and current surveys from 2004 to 2008. To estimate density for historical communities, we used the Morisita plotless density estimator and applied corrections for surveyor bias. To estimate density for current forests, we used Random Forests, an ensemble regression tree method, to predict densities from known values at plots using terrain and soil predictors. Oak species decreased from 62% of historical composition to 30% of current composition and black and white oaks historically were dominant species across 93% of the landscape and currently were dominant species across 42% of the landscape. Current forest density was approximately two times greater than historical densities, demonstrating loss of savanna and woodlands and transition to dense forest structure. Average tree diameters were smaller than in the past, but mean basal area and stocking remained similar over time because of the increase in density in current forests. Nevertheless, there were spatial differences; basal area and stocking decreased along rivers and increased away from rivers. Oak species are being replaced by other species in the Missouri Plains, similar to replacement throughout the range of *Quercus*. Long-term commitment to combinations of prescribed burning and silvicultural prescriptions in more xeric sites may be necessary for oak recruitment. Restoration of open oak ecosystems is a time-sensitive issue because restoration will become increasingly costly as oaks are lost from the overstory and the surrounding matrix becomes dominated by non-oak species.

1. Introduction

In eastern forests of the United States, a wave of widespread and intensive timber harvesting occurred over a relatively short period (e.g., 1800 to 1920) following Euro-American settlement in North America. Extensive harvest promoted oak regeneration in predominantly oak forested ecosystems through release of advance regeneration and stump sprouts (Williams, 1989; Aldrich et al., 2005). The regional scale of forest disturbance resets the age distribution and structure of oak forest ecosystems to dense oak forests by initiating oak regeneration as forests were harvested. Subsequently, suppression of fire in North America changed the disturbance regime to small-scale disturbances, which has promoted the shift to fire-sensitive species in forests of various successional stages at a large scale (Nowacki and Abrams, 2008; Hanberry et al., 2012a). Due to changes in land use, oak recruitment failure and decreasing dominance are occurring throughout eastern North American forests and worldwide (Watt, 1919; Thadami and Ashton, 1995; Humphrey and Swaine, 1997; Niklasson et al., 2002; Svenning, 2002; Li and Ma, 2003; Hofmeister et al., 2004; Götmark et al., 2005; Pulido and Díaz, 2005; Strandberg et al., 2005; von Oheimb and Brunet, 2007; Zavaleta et al., 2007; Hédl et al., 2010; Altman et al., 2013). As a consequence, some light-demanding herbaceous plants,

* Corresponding author. Tel.: +1 573 875 5341x230; fax: +1 573 882 1977.
E-mail address: hanberryb@missouri.edu (B.B. Hanberry).
[1] Tel.: +1 573 875 5341x230; fax: +1 573 882 1977.

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http://dx.doi.org/10.1016/j.scitotenv.2014.01.048

and associated wildlife, saproxylic insects, epiphytes, and fungi of open oak ecosystems are declining along with oaks (McShea et al., 2007; Rogers et al., 2008; Lindbladh and Foster, 2010). Oaks, a foundation genus, provide open forested structure, which has become an increasingly rare vegetation type, resulting in biodiversity changes to species that succeed under intensive land use or in closed forests.

The Missouri Plains, in the central United States, are part of the prairie peninsula (Transeau, 1935), a grassland extension into eastern broadleaf forests, where a mosaic of prairies, savannas, woodlands, and forests historically intermingled in patterns influenced by the interaction of soils, topography, and fire disturbances (Nigh and Schroeder, 2002). Prairies were present on flat plains and broad ridges exposed to annual or near-annual fires, oak savannas and woodlands occurred where topographic roughness or wetlands extended fire-free periods to probably at least 5 years, and forests were common on lower and rough slopes and near wetlands including stream networks protected from fire (Nigh and Schroeder, 2002). Stambaugh et al. (2006) reported a mean fire interval of 6.6 years before substantial Euro-American settlement around 1820 in the loess hills of northwestern Missouri. A fire regime that was frequent but not annual favored fire-tolerant oak species and the open structure of savannas and woodlands (Bond et al., 2005). Oak savannas and woodlands had open or simple canopies and fire removed midstories, permitting sufficient light to reach the ground to support a diverse ground cover of forbs and grasses (Nuzzo, 1986).

During the past 150 years, human culture and land use have changed in the Missouri Plains. The final transfer of Osage lands in Missouri by treaty to the US government in 1825 (Rollings, 1992) represented a historical shift in land ownership from Native American to European occupation and use. Stambaugh et al. (2006) observed that the mean fire interval decreased to 1.6 years during initial Euro-American settlement (1825–1850). The use of fire as a tool was continued by Euro-American settlers; in fact, fires were more frequent during initial Euro-American settlement. However, increased development and human densities led to fire suppression by the 1920s. Since the 1950s, wildfires have become rare and average about 4 ha in size during non-drought years in the Missouri Plains region (Westin, 1992). Agricultural development rapidly increased in the midwestern US, including Missouri, as corn and wheat farming developed between 1850 and 1910 (Ramankutty and Foley, 1999). Prairies, savannas, and woodlands of the Missouri Plains were converted to pasture and crop fields (Schroeder, 1981; Ramankutty and Foley, 1999). Later, farm abandonment that occurred during 1930 to 1990 initiated old field succession (Ramankutty and Foley, 1999).

Today, less than 1% of the original savannas in the midwestern prairie peninsula region remain due to conversion to intensive and extensive agriculture and grazing or rapid transition to (relatively) closed canopy forests following fire suppression (Nuzzo, 1986). Although oak forests still dominate xeric sites, oaks are declining on higher quality sites throughout eastern North America and communities are shifting to a range of fire-sensitive species that once were confined to sites protected from fire (Nowacki and Abrams, 2008; Fralish and McArdle, 2009; Hanberry et al., 2012a). Current forest densities and composition show less variation along large scale ecological gradients than in the past due largely to fire suppression and land use events such as exploitative logging and the conversion of forestlands to agriculture and subsequent agricultural abandonment; however, at small scales logging and land abandonment may produce a very high contrasting structure and composition (e.g., edges; Williams, 1989; Hanberry et al., 2012a, 2014).

Although there is a conceptual process of how eastern forests have changed over the past 100 to 150 years (Williams, 1989), there is little quantitative research on historical forest conditions and how they have changed in current times in the Missouri prairie peninsula region. To quantify historical forests, we used General Land Office (GLO) records from the Missouri Plains as a reference for historical forest communities and densities immediately before Euro-American settlement. To determine long term and large scale changes, we compared historical values to current forest communities and densities from USDA Forest Inventory and Analysis (FIA). In addition to the provision of 1) historical ranges of structural values and 2) large scale forest change over time, we present management approaches to address widespread decrease of oak dominance in the eastern United States that may be useful in other regions with oak dominance declines.

2. Methods

2.1. Ecological units

The Missouri Plains cover about 8 million ha and are located in the northwestern part of Missouri (Fig. 1). The Missouri Plains are composed of two ecological sections, the Osage and Till Plains, and further divided into ecological subsections by climate, soils, topography, vegetation, and then divided into land types, such as hills or plains (Nigh and Schroeder, 2002; Fig. 2). We used ecological units, composed of ecological subsections divided into land types, to provide a detailed spatial range of communities and densities across the landscape.

2.2. Community rules

We grouped some tree species into the following categories primarily because of genus-only identification in the GLO surveys: ashes (*Fraxinus americana*, *Fraxinus pennsylvanica*); cherries (*Prunus* spp.); elms (*Ulmus alata*, *Ulmus americana*, *Ulmus rubra*); hickories (*Carya cordiformis*, *Carya glabra*, *Carya laciniosa*, *Carya ovata*, perhaps *Carya texana* and *Carya tomentosa*); maples (primarily *Acer saccharum*, *Acer negundo*, *Acer saccharinum*); red oaks (*Quercus rubra*, *Quercus falcata*, *Quercus coccinea*); walnuts (*Juglans nigra*, *Juglans cinerea*); cottonwoods and willows (*Populus* spp., *Salix* spp.); and mulberry and locusts (*Morus rubra*, *Robinia pseudoacacia*, *Gleditsia triacanthos*).

To determine community composition, we set a threshold of ≥200 trees per ecological unit, resulting in a total of 14 units that met that threshold during each time period (Appendix A). To be classed as a dominant species in a community, percent composition (of species) had to be ≥10% per ecological unit in order to limit communities to no more than 6 species/species groups and yet have species representation. The order of tree species reported within a community was based on descending mean percent composition for all GLO trees to make comparisons more straightforward. For example, black oak had the overall greatest percent composition across all ecoregions and was therefore the first species listed where it exceeded >10% in composition.

2.3. Current surveys and forest density

Every five years, the USDA Forest Inventory and Analysis program surveys long-term forest plots located about every 2400 ha across the country. Each plot contains four 7.31 m radius subplots, configured as a central subplot surrounded by three outer subplots. We used data from the latest complete cycle of 2004 to 2008. We selected live trees with a diameter ≥12.7 cm to correspond with diameters present in GLO surveys; additionally, smaller diameter trees are surveyed in a fraction of each subplot. We selected plots that were 100% forestland, which FIA defines as land at least 1 acre in area and 120 ft wide with at least 10% cover by live trees of any size, "including land that formerly had such tree cover and that will continue to have forest use", and contained at least two trees to exclude some plots that were harvested recently. We calculated trees per hectare using the supplied FIA expansion factor of 6.02 (i.e., one tree represents the inverse of the plot area in acres; $1 / (4 * 0.042)$), and summed the values for each plot.

To predict total density from discrete plots to a continuous surface, and ultimately comparable to historical densities, we used Random Forests regression trees (Breiman, 2001; Cutler et al., 2007) with the